Neuroscience and Biobehavioral Reviews 78 (2017) 161–177

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

Memory scrutinized through electrical brain stimulation: A review of 80 years of experiential phenomena

Jonathan Curot[a,b,*], Thomas Busigny[a], Luc Valton[a,b], Marie Denuelle[a], Jean-Pierre Vignal[c], Louis Maillard[c,d], Patrick Chauvel[e,f], Jérémie Pariente[a,g], Agnès Trebuchon[e,f,h], Fabrice Bartolomei[e,f,h], Emmanuel J. Barbeau[b]

[a] Department of Cognitive Neurology, Epileptology and Movement Disorders, Toulouse University Hospital, France
[b] CerCo, CNRS, UMR5549, Toulouse Mind and Brain Institute, France
[c] Department of Neurology, Nancy University Hospital, France
[d] University of Nancy, France
[e] INSERM, U751, Marseille, France
[f] Faculty of Medicine, Aix-Marseille University, France
[g] INSERM, U1214, TONIC, Toulouse Mind and Brain Institute, France
[h] Department of Clinical Neurophysiology, Marseille University Hospital, France

ARTICLE INFO

Keywords:
Memory
Reminiscence
Electrical brain stimulation
Experiential phenomena
Episodic memories
Semantic memories
Autobiographical memory
Rhinal cortex
Hippocampus
Epilepsy

ABSTRACT

Electrical brain stimulations (EBS) sometimes induce reminiscences, but it is largely unknown what type of memories they can trigger. We reviewed 80 years of literature on reminiscences induced by EBS and added our own database. We classified them according to modern conceptions of memory.

We observed a surprisingly large variety of reminiscences covering all aspects of declarative memory. However, most were poorly detailed and only a few were episodic. This result does not support theories of a highly stable and detailed memory, as initially postulated, and still widely believed as true by the general public.

Moreover, memory networks could only be activated by some of their nodes: 94.1% of EBS were temporal, although the parietal and frontal lobes, also involved in memory networks, were stimulated. The qualitative nature of memories largely depended on the site of stimulation: EBS to rhinal cortex mostly induced personal semantic reminiscences, while only hippocampal EBS induced episodic memories. This result supports the view that EBS can activate memory in predictable ways in humans.

1. Introduction

In 1934, Penfield reported that the application of low intensity electrical brain stimulation (EBS) on specific portions of the cortex of an epileptic patient undergoing awake neurosurgery made him/her relive an event of his/her past. Between the 30s and 60s, Penfield reported 40 epileptic patients who experienced psychic phenomena after application of EBS on the neocortex (Penfield, 1958; Penfield and Perot, 1963). Among them, several patients reported reminiscences of past experiences. Penfield assimilated these responses to the dreamy-state occurring spontaneously during seizures described half a century earlier by Hughlings Jackson (1880) and Hughlings Jackson and Colman (1898) (Box 1). Penfield considered that EBS were reactivating complete stored memory traces, these experiential phenomena being viewed as replays of engrams, like a "tape-recording": "*Past experience, when it is recalled electrically, seems to be complete including all the things of which an individual was aware at the time […]*" (Penfield and Perot, 1963).

Since Penfield's pioneering work, several studies have also reported experiential phenomena after EBS (see below for a complete list). However, some of them challenged Penfield's theory. For example, Gloor (1990) proposed the matrix theory, a reconstructive process whereby EBS leads to the elaboration of excitation and inhibition patterns in widely distributed neural networks, of which some are able to represent a given previous experience, albeit in a caricatured way. Hence, whereas Penfield thought that EBS could induce reminiscence exactly similar to the original event, a bit like playing a videotape at random, Gloor was of the view that only the gist of these memories could be activated. Penfield's hypothesis remains influential nowadays (Loftus and Loftus, 1980; Simons and Chabris, 2011). But although attractive, whether this conception of a highly stable memory is

Abbreviations: AD, afterdischarge; EBS, electrical brain stimulation; SEEG, stereoelectroencephalography

* Corresponding author at: CerCo UMR5549, Pavillon Baudot, CHU Purpan, BP25202, 31052 Toulouse Cedex, France.
E-mail address: jonathan.curot@cnrs.fr (J. Curot).

http://dx.doi.org/10.1016/j.neubiorev.2017.04.018
Received 1 November 2016; Received in revised form 16 March 2017; Accepted 19 April 2017
Available online 23 April 2017

Box 1
Definitions

We provide in this box a definition for some of the technical terms used in this review.

Afterdischarge: Transient EEG changes after electrical brain stimulation (EBS), easily observed on intracranial recordings and corresponding to a burst of epileptiform activity induced by the electrical stimulation. An afterdischarge can be confined to the electrodes that are stimulated, but it can also spread to other brain areas, with or without clinical symptoms. When an afterdischarge spreads to other adjacent and remote electrodes, it can be considered as a stimulation-EEG induced seizure. EBS applied during SEEG or electrocorticography do not systematically induced afterdischarges (see Kovac et al., 2016 for review).

Déjà-vu: A transitory mental state whereby an objectively novel experience feels subjectively familiar. This experiential phenomenon is devoid of any content and has a short time course (Illman et al., 2012).

Dreamy-state: This terminology was originally used by Hughlings-Jackson (1880, 1888, 1898) to define a particular "elaborate and voluminous" mental state that occurs during some epileptic seizures: "*There is not always loss, but there is, I believe, always, at least defect, of consciousness co-existing with the over-consciousness*" (1898), "*I believe—there is a kind of double consciousness—a 'mental diplopia',"* (1899). He hypothesized that these mental states were "of different kinds". He paradoxically never referred specifically to dreams, but rather emphasized the fact that experiential phenomena following temporal lobe epilepsy felt like dreaming. Today, in clinical practice, experiential phenomena (see definition) related to temporal lobe epilepsy are often grouped under the term "dreamy-state", although reminiscences or experiential phenomena seem more appropriate because better defined.

Electrical Brain Stimulation: It is the application of electrical current directly to the cortex. It can be delivered temporarily: intra-operatively during awake surgery in patients with brain tumours or intractable epilepsy to identify critical areas for cognitive and motor functions; extra-operatively during stereoelectroencephalography and electrocorticography (see definition) in patients with intractable epilepsy in order to study connectivity, cortical excitability and to delineate the seizure onset zone. It can also be delivered chronically with implanted electrodes for treating various neurological (Parkinson disease, essential tremor, under development for intractable epilepsy) and psychiatric disorders (depression, obsessive compulsive disorders). They can sometimes induce unexpected behaviours and experiences, such as reminiscence (see definition).

Electrocorticography: Intracranial recording of EEG with similar indications and goals as the SEEG (see definition), but in this case subdural grids are placed directly on the surface of the cortex to record electrical activity from the cerebral cortex. A craniotomy is required to implant the grids. Recordings can be performed either in the operating room or extra-operatively during several days. Low intensity currents can be delivered between adjacent contacts to study local cortical excitability.

Experiential phenomena: This term is used in a broad sense and includes various types of transitory mental states, sensory and memory illusions, which the patients subjectively experience. They can occur during an epileptic seizure or following electrical brain stimulation. Penfield (1954) was the first to use the word "*experiential*": initially "*experiential flash-back*" referred to the "*random re-enactment of a conscious sequence from the patient's past"*. It was separated from "*interpretive illusions"* which referred to "*alteration of perception of the present"* such as auditory illusions and from "*interpretive signaling"* which were "*production of sudden interpretations of the present experience, such as familiar, strange, fearful…"*. Gloor gathered all these as "*experiential phenomena*" (Gloor et al., 1982; Gloor, 1990).

Reminiscence: Involuntary recall of a memory during a seizure or following electrical brain stimulation. This phenomenon has content such as visual mental images and/or other sensory characteristics contrary to déjà-vu. The time course of this phenomenon is supposed to be longer than déjà-vu. The content can refer to different type of information and thus to different types of memories: semantic memories, personal semantics, episodic memories but also reminiscences of dreams. Hughlings Jackson (1888) also used the word "*reminiscence*". But he assimilated it to the "*dreamy-state*" and he never defined it explicitely.

Stereoelectroencephalography (SEEG): Intracerebral and extra-operative recording of EEG during several days long, using depth electrodes surgically implanted into the brain. SEEG is used for drug-refractory epileptic patients, candidates for neurosurgery. Noninvasive presurgical assessment could not determine precisely the seizure onset zone. Intracerebral electrodes are thus implanted using a stereotaxic frame in circumscribed brain areas according to seizure semiology and hypothetical epileptic networks. The patient keeps these electrodes until seizures occur to determine the seizure onset zone. Low intensity currents can also be delivered along the different contacts of the electrodes to study local excitability (Talairach and Bancaud, 1965).

plausible or whether it is one of the numerous neuromyths that have been identified remains to be clarified (Lilienfeld et al., 2009; Dekker et al., 2012). This situation is largely due to the fact that it is unknown what type of memory EBS can exactly induce.

Furthermore, divergent views can be found in the literature about the influence of the localization of EBS (Penfield, 1958; Halgren et al., 1978; Vignal et al., 2007; Bartolomei et al., 2004). For example, some authors consider that the site of stimulation has no consequence on the type of memory induced, favouring the idea that what matters is the patients' personality (Halgren et al., 1978; Halgren and Chauvel, 1993; Chauvel, 2014), whereas others suggest that stimulation of specific sites could induce specific types of memories (Bartolomei et al., 2004; Barbeau et al., 2005). However, these reminiscences are nowadays the major source of inspiration for preliminary trials aiming at improving memory performances using EBS (Lee et al., 2013; Suthana and Fried, 2014). A series of reports demonstrated that EBS of the medial temporal lobes but also of the fornix could induce memories (Halgren et al., 1978; Gloor et al., 1982; Bancaud et al., 1994; Gloor, 1990; Hamani et al., 2008; Vignal et al., 2007). It is for this reason that stimulation of the rhinal cortex (Suthana et al., 2012, Fell et al., 2013), hippocampus (Fell et al., 2013) or fornix (Laxton et al., 2010; Smith et al., 2012; Fontaine et al., 2013) were chosen empirically as targets to modulate memory networks using chronic EBS. Whether the site of EBS really has no consequence on the type of memory; or whether there is a preferable localization to access specific types of memory is thus of crucial importance to determine how to modulate memory using EBS.

Moreover, an important variability of electrical stimulation parameters (electrode geometry, pulse amplitude, duration, frequency, monopolar or bipolar EBS, monophasic or biphasic pulses) can be found in the literature. This variability leads to differences in the electric field distribution (Kuncel and Grill, 2004; Winawer and Parvizi, 2016) and make it uncertain which neural elements are really targeted and modulated by EBS across studies. Fundamental questions remain about the effects of EBS on the neurons surrounding the electrode and